J. Malac. Soc. Aust. 6(3-4): 101-111

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Distribution and feeding of chitons in a boulder habitat at West Island, South Australia

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ABSTRACT

The vertical distribution and feeding of sixteen species of chiton was examined on a boulder slope at West Island, South Australia. There is a trend of increasing abundance and diversity of species with depth, with most species present at 4-5 m depth where boulders are partly buried by sediment.

Six species are herbivorous, seven omnivorous and three carnivorous. There are generalist and specialist feeders within those feeding types. Specialist feeders include species which eat predominantly drift seagrass (one species), crustose coralline algae (four species), *Petroderma* crusts (one species), sponge (one species) and amphipods (one species).

A comparison of the distribution with depth of abundance of food organisms attached to the upper and under-surface of boulders with the depth distribution of chitons, shows that the food supply is unlikely to limit the abundance of chitons or affect their distribution. However, drift seagrass and algae, eaten by several species, are abundant only at 4-5 m depth; this may be a factor contributing to the abundance of some chitons at this depth.

INTRODUCTION

Subtidal crevice faunas and floras, although rarely studied, are ecologically important because crevices provide a refuge and a place for recruitment of many mobile species, including those of economic value such as abalone and sea urchins (Shepherd 1973; Tegner and Dayton 1977, 1981; Brock 1979).

Chitons are prominent members of the mobile fauna of crevices, and in southern Australia, the chiton fauna is notably rich in species (Hyman 1967, Boyle 1977). Chitons have usually been considered to be herbivorous grazers (Simpson 1976, Boyle 1977, Steneck and Watling 1982), although omnivory and even carnivory are known to occur (Barnawell 1969, McLean 1962, Langer 1983).

A boulder slope in Abalone Cove, West Island, South Australia (35°36′25″S., 138°35′27″E.) (Fig. 1) has an over-boulder flora of erect and crustose algae, and an under-boulder sessile fauna of crustose sponges, bryozoans, and ascidians and a mobile fauna of chitons and gastropods. The chitons, in particular, are numerically abundant and diverse, with 22 species present.

This study is part of an investigation of the role of chitons in this complex community whose biological interactions are of likely importance. The broad components of the habitat above and below boulders, the distribution and density of chitons along a depth gradient, and the diet of 16 chiton species are described and the diet related to the presence and abundance of food in the habitat. The algal ecology of West Island is described by Shepherd and Womersley (1970).

MATERIALS AND METHODS

Distribution and Abundance of Organisms

The north shore of Abalone Cove, West Island, is a boulder slope containing boulders, mostly 30-40 cm × 20-30 cm and 20 cm high, from about 0.5 m depth to 5 m at low water. At six depth intervals (0.5 m and at 1 m depth intervals from 1 to 5 m), 20 boulders taken from different locations along the boulder slope were overturned and the chitons on the under surface and on rocks below the boulder were identified and counted. In order to estimate the density of chitons, the area of each boulder was taken to be its projection on the horizontal plane. In addition, exhaustive searches were made over the depth range for less common species. Estimates of the mean percentage cover of crustose organisms on and under boulders were obtained by laying a transparent sheet of plastic marked with a 2.5 cm grid on the boulder and counting the number of squares occupied by each organism. Estimates of cover of upper (>20 cm high) and middle (1-20 cm) algal strata on the upper side of boulders were also made.

Food and Feeding

Samples of each species of chiton were collected between January and April 1983, and preserved in 10% formol seawater. The whole of the digestive tract, from stomach to anus, was removed from each animal, the contents spread on a slide and examined microscopically. The slide was scanned along several parallel lines and the material under the cross of the eyepiece at equidistant points was identified to morphological group. Plant material was categorised as coralline algae (geniculate and encrusting), **Petroderma* crusts, filamentous algae, macroalgae and seagrasses, in accordance with the functional scheme proposed by Steneck and Watling (1982). Animal matter was placed in one of the following taxonomic groups: sponge, bryozoans, ascidians, hydroids, serpulid worms and amphipods. According to the amount of food in the gut, 20-90 identifications of food items were made for each individual. The basis for evaluating the accuracy of the method is given by Curtis (1960). Shepherd and Boudouresque (1984) tested the accuracy of the method experimentally and showed that gains in accuracy decline sharply after 50 identifications, so do not justify additonal effort.

Within species differences in the food eaten with depth were examined for four species by analysing the gut contents of five individuals per species at different depths. The differences were analysed statistically with the non-parametric Mann-Whitney U-Test.

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* This refers to crusts of non-calcified algae, mostly of an undescribed species of the genus *Petroderma*.

A night dive was made on 24 February 1983 and the species on the upper surfaces of boulders noted.

RESULTS

The Boulder Habitat

The boulder slope at West Island has an upper stratum of *Ecklonia radiata* and *Cystophora monilifera* from about 2-5 m depth (Fig. 1), with a middle stratum of geniculate corallines mostly from 4-5 m depth.

The distribution of mean percentage cover of algae of the middle and lower (i.e. crustose) strata with depth on the upper surfaces of boulders is shown in Fig. 2, and of crusose organisms on the under surfaces of boulders in Fig. 3. Upper surfaces of boulders have an almost 100% cover of encrusting algae and geniculate corallines often below the canopy of *Ecklonia* and *Cystophora,* whereas the under surfaces have a somewhat diverse encrusting fauna and flora with a total cover of 50-90% (Fig. 3).

Distribution and Feeding of Chitons

Twenty-four species of chiton occur subtidally and one species intertidally. Sixteen species examined by us are listed in Table 1 according to feeding type, together with data on depth range, mean density, size range and number of gut contents analysed. The remaining nine species are listed in the Appendix, but they were either too rare to allow feeding studies of them or were in seagrass. The vertical distribution of the more abundant species is shown in Fig. 4. The number of species is least in shallow water, but increases with depth, so that at 4-5 m depth where boulders are partly buried in sediment, most species are present and attain their highest density.

However, *Ischnochiton australis,* and to a lesser extent, *Ischnochiton elongatus* and *Chiton calliozonus,* have lower densities at intermediate than in deeper or shallower depths. The decrease in density of these species was not an artifact of sampling because replicate samples at 3 m depth gave the same results.

The proportion of different food organisms in the gut of sixteen species of chiton is shown in Figs. 5-7. Six species are herbivorous, with 75% or more of plant material in the gut (Fig. 5). They include generalist feeders *(I. australis, I. cariosus* and *Plaxiphora albida)* and specialist feeders *(Ischnochiton torri, Chiton diaphorus* and *Callochiton crocinus)* wich feed predominantly on seagrass, crustose corallines, and *Petroderma* crusts respectively.

Omnivorous species (Fig. 6) eat both plant and animal matter. In three of them *(C. calliozonus, Chiton torrianus,* and *Chiton tricostalis),* the diet is predominantly crustose coralline algae. The remaining four species *(Ischnochiton elongatus, Ischnochiton lineolatus, Cryptoplax striata* and *Lorica cimolia),* show more diversity in the kind of food eaten and variabilty in their proportions within species. Hence it is likely that these species are generalists which feed opportunistically according to the local availability of food.

Three species are mainly carnivorous (Fig. 7), with 75% or more of animal material in the gut. *Notoplax speciosa* is almost exclusively a sponge feeder, *Ischnochiton smaragdinus* eats bryozoans and ascidians as well as sponge. *Loricella angasi* feeds largely on amphipods, but also consumes other animal and plant material. According to Ludbrook and Gowlett (1984) the latter species traps amphipods by rapidly clamping the previously elevated girdle to the substate.

Four species (Table 1) crawl on to the upper surfaces of boulders at night, and a fifth, *I. australis,* on to the sides of boulders, presumably to feed. The remaining species are cryptic, by night as well as by day.

Differences with depth in the proportions of major food categories eaten were examined for four species. The differences were significant for one or more food categories in three species (Table 2). Drift seagrass (mostly *Heterozostera tasmanica)* is only abundant at 5m depth and the availablity of this appears to largely account for the differences in the diet of *I. australis, I. cariosus* and *I. lineolatus* with depth.

DISCUSSION

In a recent review, Steneck and Watling (1982) suggested that chitons are herbivores which largely specialise on perennial (leathery) macrophytes or crustose corallines. This overlooks numerous earlier studies, summarised by Boyle (1977), which show that some chitons may consume considerable amounts of animal matter. This is the first account of the distribution and diet of a chiton 'guild' in Australian waters, and it shows an astonishing diversity of species, with a wide variety of feeding types co-existing over a narrow habitat range. The feeding types include herbivores, omnivores and carnivores, and there may be generalist or specialists within those categories. Of special interest is the carnivorous species, *L. angasi,* which captures live amphipods; this has otherwise been recorded only for the Californian species, *Placiphorella velata,* Dall (McLean 1962).

Food resources on the boulders (attached algae and crustose animals) are abundant at all depths and apparently more than sufficient for the chiton populations dependent on them. Hence food is unlikely either to limit the abundance of these species or influence their distribution. An exception is drift seagrass, which only occurs at 4-5 m depth. *I. torri,* a specialist feeder on this resource, occurs only at these depths, and may thus be one species whose vertical distribution is limited by the distribution of its preferred food.

The low abundance of *I. australis* at intermediate depths on the boulder slope (Fig. 4) is enigmatic. The unusual escape behaviour of this species which curls up and falls off a rock if disturbed (Ludbrook and Gowlett 1984), would enhance their survival of individuals when boulders are rolled about during storms, and may account for the abundance of this species in very shallow water.

It is surprising that only four species emerge at night apparently to feed. Presumably there is an abundant supply of food on the undersides of boulders for the other species, so that they do not need to make feeding excursions.

The abundance and diversity of chitons at 4-5 m depth may be due in part to their apparent preference for a habitat under boulders partly buried in sediment, and partly to the abundance of drift algae and seagrasses, which a majority of these chitons eat.

Some authors (Adey 1973, Steneck 1977, Brock 1979, Paine 1980) have suggested that grazing may be important in maintaining the stability of crustose communities by enhancing the growth of competitively inferior species such as coralline algae, or removing superior competitors for space such as ascidians. The wide range of feeding types present among these chitons shows that they are capable of doing so but whether they in fact do so is currently being examined by manipulative experiments.

ACKNOWLEDGEMENTS

We are grateful for field assistance from Ms. Jean Turner and Mr. P. Clarkson. Professor H.B.S. Womersley kindly identified the *Petroderma* crusts and Miss Karen Gowlett gave much helpful advice on the taxonomy of chitons, and wrote the Appendix.

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Table 1. List of species of chitons on the boulder slope at West Island, with depth range, mean density, mean size and size range, and number of gut contents analysed.

Species	Depth Range (m)	Mean Density (Nos. m^{-2}	Length (mm) Range Mean	Number used in Feeding Study

Herbivores				
Ischnochiton (Ischnoradsia) australis (Sowerby)	0.5-5	19.4	29-57 43.1	25
Ischnochiton (Heterozona) cariosus Carpenter	2-5	6.3	24-37 29.5	20
Ischnochiton (Autochiton) torri Iredale & May	4-5	0.1	21-40 31.8	9
**Chiton (Rhyssoplax) diaphorus* (Iredale & May)	0.5-5	3.7	21-32 27.8	20
Callochiton crochinus Reeve	3-5	1.0	12-26 19.1	10
Plaxiphora albida (Blainville)	Intertidal	0.5	35-70 54.0	6
Omnivores				
Ischnochiton elongatus (Blainville)	0.5-5	6.0	18-29 29.4	10
Ischnochiton lineolatus (Blainville)	2-5	10.0	25-36 23.9	20
**Chiton (Rhyssoplax) calliozonus* Pilsbry	1-5	4.0	23-47 33.8	10
**Chiton (Rhysoplax) torrianus* Hedley & Hull	0.5-5	3.0	24-39 30.1	10
Chiton (Rhyssoplax) tricostalis Pilsbry	3-5	0.5	15-23 17.2	10
Cryptoplax striata (Lamarck)	4-5	0.1	60-70 65.0	5
Lorica cimolia (Reeve)	0.5-5	2.0	16-69 37.7	10

Carnivores				
**Ischnochiton (Haplopax) smaragdinus* (Angas)	2-4	1.5	18-25 21.3	10
Notoplax speciosa (H. Adams)	2-5	0.1	13-16 14.5	2
Loricella angasi (H. Adams)	3-5	0.1	21-47 36.7	7

* Observed above boulders during night

Table 2. Differences in feeding with depth of four species of chiton. Significance levels (Mann-Whitney U test) are shown as follows: * = $P < 0.05$; ** $P < 0.01$.

For *I. australis* the difference between 0.5 and 2.5 m were not significant; differences between 0.5 and 5 m and 2.5 m and 5 m were both significant at the level indicated.

		Mean % of Food in Gut			
Species	Depth (m)	Encrusting Coralline algae	Erect algae	Seagrass	Animal
I. australis	0.5	54.7	39.0	0	0.5
	2.5	42.4	47.1	0	3.6
	5.0	6.8*	15.7	69.6**	4.0
I. cariosus	2.5	18.0	21.9	18.3	26.7
	5.0	20.8	13.1	59.2	3.3*
I. lineolatus	2.5	50.0	26.3	14.4	3.2
	5.0	18.1	32.5	39.4	7.4
C. diaphorus	2.5	81.4	6.7	0	4.0
	5.0	97.3*	0	0	0

APPENDIX

Additions to the chiton fauna of West Island

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Ischnochiton (Ischnochiton) variegatus (H. Adams & Angas) Rare, under smooth rocks in sandy pockets, at one metre depth.

Stenochiton cymodocealis Ashby. On seagrass *Amphibolis antarctica* at base of stems, usually buried in sand, at 5 m depth.

Stenochiton longicymba (Blainville). Under stones among seagrass beds of *Posidonia sinuosa*, at 5 m depth. This species is usually found in the leaf sheath of the seagrass.

Callistochiton antiquus meridionalis Ashby Rare, usually under bare rocks at 3-5 m deep.

Plaxiphora (Fremblya) matthewsi Iredale Usually under rocks in silty situations, at 5 m depth.

Cryptoplax iredalei Ashby Rare, in Abalone Cove, at 3 m depth.

Acanthochitona gatliffi (Ashby) Rare, under rocks at 3 m deep.

Acanthochitona pilsbryi (Sykes) Rare, under rocks in sponge at 2-3 deep.

Acanthochitona suerii (Blainville) Rare, under rocks in sponge at 2-3 m deep.

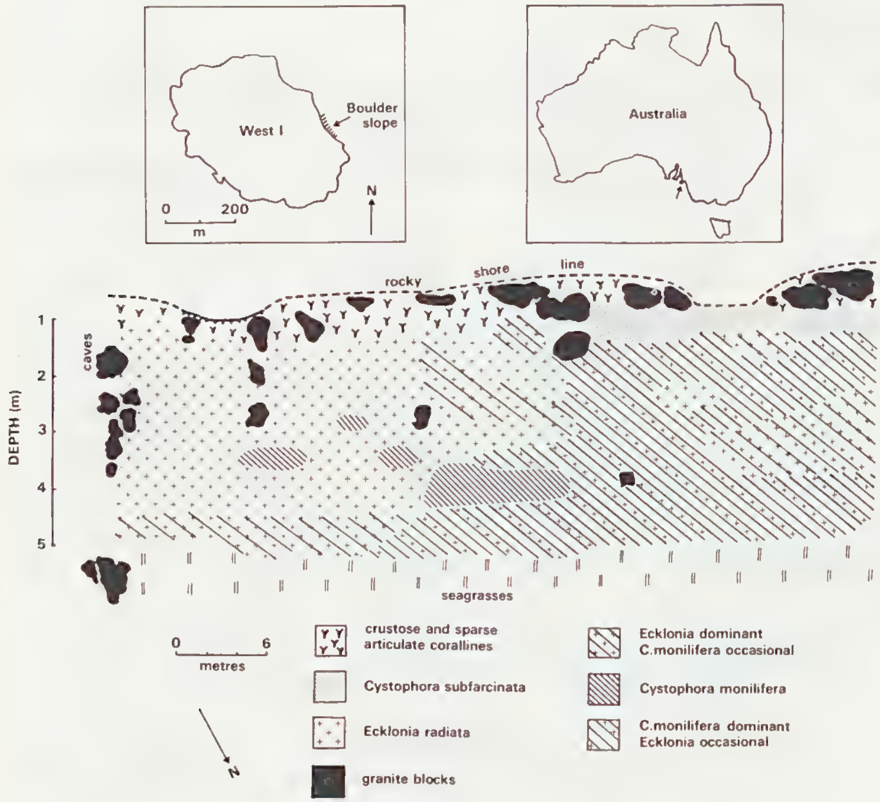

Fig. 1. Map of West I. and of the algal communities of the boulder slope in Abalone Cove.

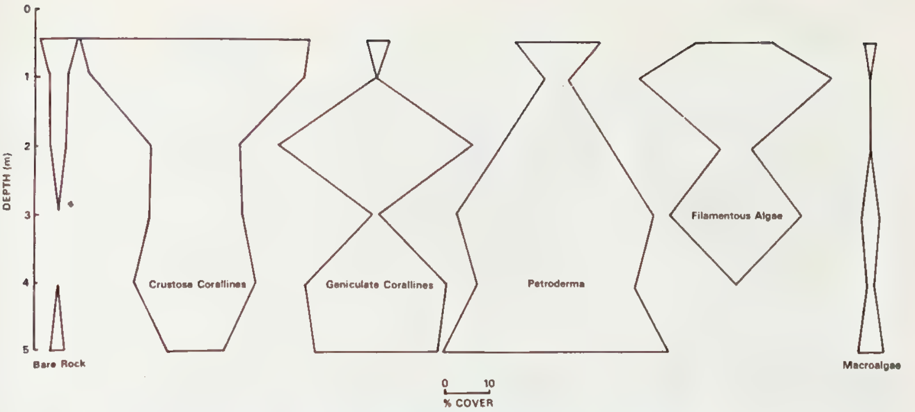

Fig. 2. Distribution with depth of mean percentage cover of middle and lower strata on the upper surfaces of boulders in Abalone Cove, West I.

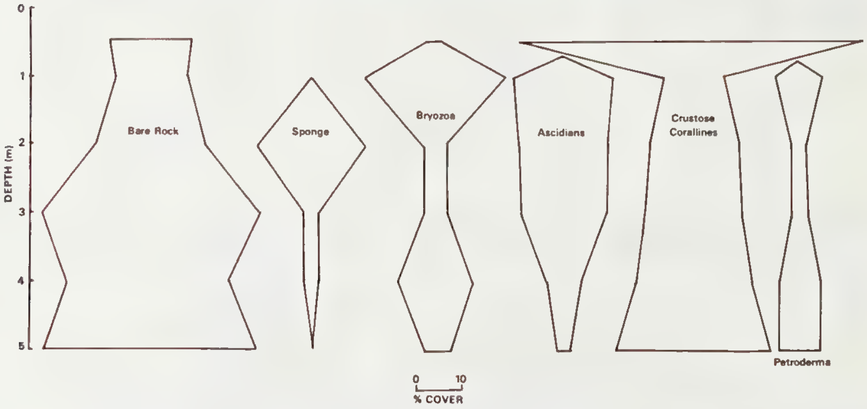

Fig. 3. Distribution with depth of mean percentage cover of crustose organisms on the under surfaces of boulders in Abalone Cove, West I.

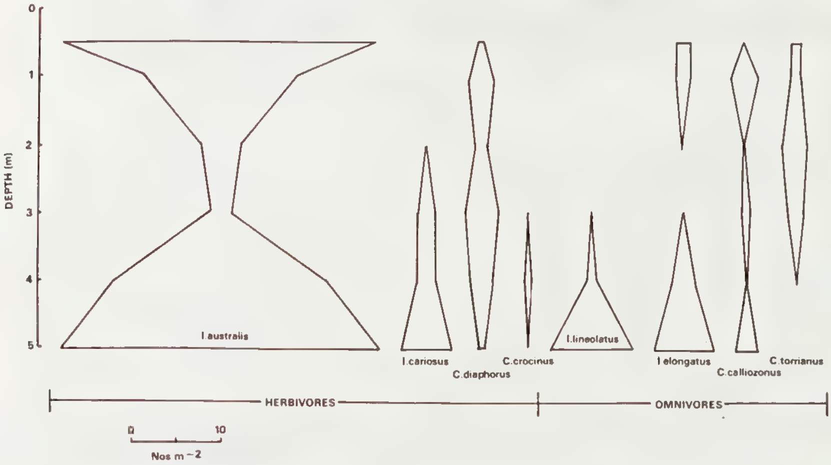

Fig. 4. Distribution of density of chitons on the boulder slope at West I.

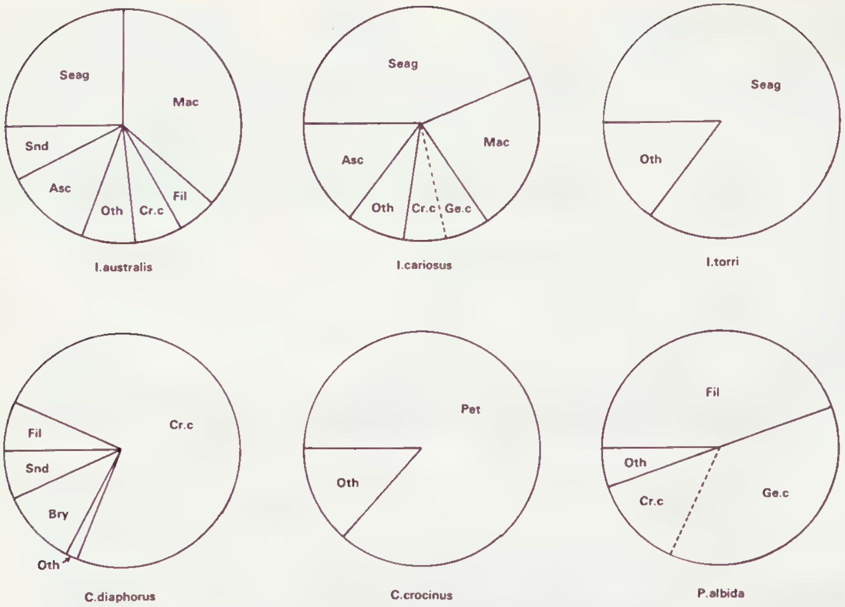

Fig. 5. Mean percentage compostion of food categories in the gut of six species of herbivorous chitons.

Cr.c : Crustose corallines
Ge.c : Geniculate corallines
Fil : filamentous algae
Mac : macroalgae
Seag : seagrass
Pet. : *Petroderma*

Snd : Sand grains
Asc : ascidians
Bry : bryozoans
Oth : other
Spo : sponge

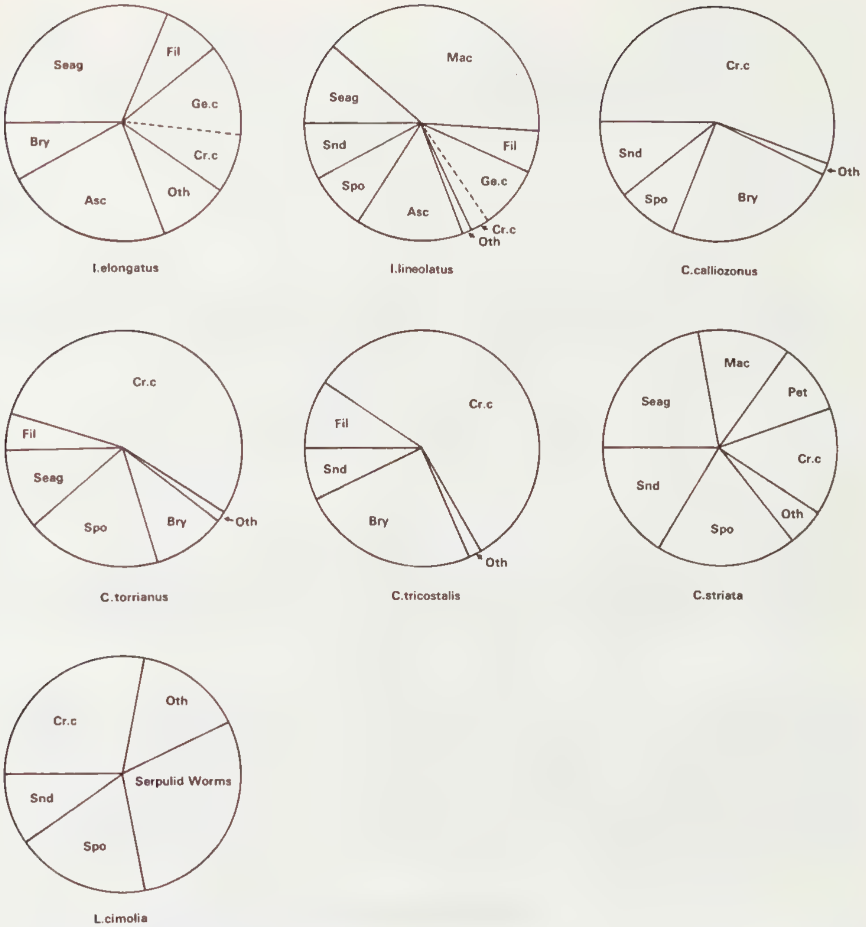

Fig. 6. Mean percenage composition of food categories in the gut of seven species of omnivorous chitons.

Notation as in Fig. 5.

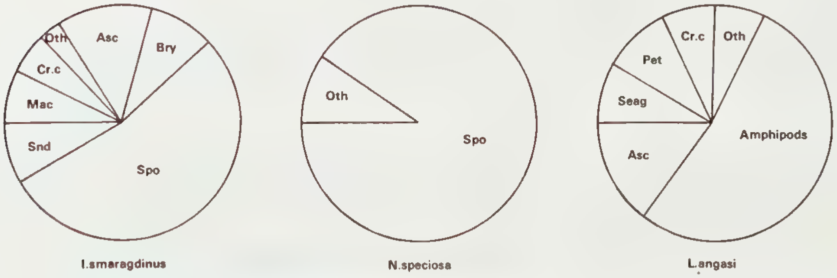

Fig. 7. Mean percentage composition of food categories in the gut of three species of carnivorous chitons.

Notation as in Fig. 5.